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Characteristics of monarch butterflies (*Danaus plexippus*) that stopover at a site in coastal South Carolina during fall migration

John W. McCord[1] and Andrew K. Davis[2*]
[1]South Carolina Department of Natural Resources, Box 12559, Charleston, SC 29422
[2]Odum School of Ecology, The University of Georgia, Athens GA 30602
akdavis@uga.edu

Abstract. While the annual fall migration of eastern North American monarch butterflies (*Danaus plexippus*) to wintering sites in central Mexico is a well-known and frequently-studied phenomenon, one aspect of this behavior that remains poorly understood is the nature of their migratory stopovers. Like migrating birds, monarchs must stop frequently during their journey to rest and refuel (i.e. obtain food), and why they choose to stop and for how long are important pieces of information, yet these have rarely been examined for monarchs. In this study we utilized data from a long-term monarch migration tagging operation in South Carolina to address certain aspects of this knowledge gap. Monarchs are tagged at this site each fall and recaptured individuals are also noted. Here we compared the characteristics of these recaptured individuals (n=407 over 13 years) to those that were never recaptured (n=12,989), focusing specifically on their wing size and wing condition, which was scored on a 1-5 scale. We also looked for evidence that stopover lengths are influenced by size or condition. The overall recapture rate at this site was 3.1%, although there was a small degree of annual variation in this rate (ranging from 1.3 - 5.6%). Males were recaptured twice as often as females. Recaptured monarchs did not differ from non-recaptured monarchs in wing size, but did have greater wing damage and wear than non-recaptured individuals. The recapture rate was the highest (8.5%) for monarchs with the most worn and damaged wings, while the rate was the lowest (2.9%) for monarchs with the freshest wings with no damage. Furthermore, monarchs with highly damaged and worn wings tended to remain longer at the stopover site than those with no damage or wear. Taken together, these results indicate that wing condition influences whether or not monarchs remain at a stopover site and for how long. In addition, they suggest that monarchs with poor wing condition may have a slower pace of migration owing to their more frequent and longer stopovers.

Key words: Monarch butterfly, *Danaus plexippus*, migration, stopover, tagging, wing condition.

Introduction

Among the Lepidoptera, monarch butterflies (*Danaus plexippus*) in eastern North America are unique because of their spectacular, annual migration to a series of overwintering sites in the mountains of central Mexico. Each fall, the last summer generation of monarchs undertakes this journey, which lasts over two months, and spans over 3000km (Oberhauser & Solensky, 2004). Like migratory birds, monarchs must make frequent stops along the way ('stopovers') to rest and/or forage for food (nectar), which is transformed into fat reserves (Brower *et al.*, 2006). As it is with migrating birds (e.g. Moore *et al.*, 1995; Hutto, 1998; Mehlman *et al.*, 2005), such stopovers are likely extremely important to the successful migration of this cohort, since monarchs utilize accumulated fat reserves both as fuel for the migratory flight, as well as to sustain themselves during the overwintering period (Alonso-Mejia *et al.*, 1997). Despite their obvious importance however, there has been very little empirical research on the nature of monarch stopovers (Davis & Garland, 2004). As such, we still have only a rudimentary understanding of how stopover sites are utilized by monarchs.

As in ornithological research projects, to study stopover of migrating monarchs, individuals must

*Corresponding author

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be captured, marked, and an effort must be made to re-observe or recapture the marked individuals at the stopover site (Davis & Garland, 2004). This allows researchers to identify the individuals that stay at the site for a lengthy period (a long stopover), versus those that are not recaptured, and are assumed to have left shortly after initial capture. Recapturing individuals also allows for estimation of the duration of stopover (i.e. the number of days between initial capture and recapture), which in itself can provide information as to the importance of the resources at the site (e.g. Cherry, 1982; Moore & Simons, 1992; Morris *et al.*, 1996; Carlisle *et al.*, 2005), and the individual variation in energetic requirements. For example, when a migrating bird's fat stores become depleted, it must stop and attempt to replenish them by foraging. And, the length of time it spends at a given site is directly related to the amount of fat it must acquire before resuming flight (e.g. Cherry, 1982; Winker *et al.*, 1992; Davis, 2001; Jones *et al.*, 2002). Thus, the stopover decisions of birds (whether to stop and for how long) are highly influenced by the condition of the individual.

Unlike migrating birds, the overall condition of a butterfly is partly dependent on the integrity of its wings. Like most butterflies, monarchs can sustain damage to their wings over time, for a number of reasons, including bird strikes, mating struggles, close contact with conspecifics during roosting, or general wear and tear with age (Leong *et al.*, 1993). Regardless of the reason, wing damage can affect flight ability in some insects (Combes *et al.*, 2010; Dukas & Dukas, 2011), and for monarchs, this could ultimately influence overall migration success. Consider that if a monarch with damaged wings has difficulty foraging, it may have to spend more time at any given stopover site to meet its energetic requirements (i.e. fat stores) for the next flight. And, if this happens at multiple stopover sites, damaged individuals would eventually fall behind. Moreover, individuals with damaged wings may also expend more energy flying, and may therefore require more frequent stopovers than would undamaged individuals. For multiple reasons then, wing 'condition' could be an important influence on stopover decisions of monarchs.

A recent study uncovered a surprising and inexplicable facet of monarch migration, that in the last 30 years, the proportion of females in the migratory generation appears to be declining (Davis & Rendon-Salinas, 2010), such that in recent collections of migrating monarchs, females make up approximately 30-35% of the migrating cohort (Brower *et al.*, 2006; Brindza *et al.*, 2008; McCord & Davis, 2010). The cause of this pattern remains unclear, but since sex ratios on the breeding grounds tend to be close to 50-50 (Herman, 1988), it is possible that something is occurring in recent years to selectively remove females from the population during the southward migration. One possibility is that females may stopover more frequently, and/or spend more time at stopover sites than do males, which, as in the case with damaged individuals, would lead to a longer overall migration, and hence greater opportunities for mortality.

The current study aims to enhance understanding of stopover biology of monarch butterflies by examining data from a long-term tagging project at a stopover site in South Carolina (McCord & Davis, 2010). Each fall since 1996, migrating monarch butterflies have been captured at this site by the lead author, who tags all butterflies (with numbered MonarchWatch stickers) and takes detailed notes on all captured individuals. By the end of 2008, he had tagged over 12,000 individuals, and importantly, he also has records of all recaptures at this site. Using these data, general patterns of migration have been examined already (McCord & Davis, 2010). Here, we use these data (from 1997-2008) to examine in detail the individuals that were recaptured by JWM after initial capture and release. These individuals represent monarchs undertaking a stopover. Thus, the primary goal of this project was to determine the characteristics of monarchs that stopover at this site. Specifically, we asked do these monarchs differ in terms of size (wing length) or wing condition from those monarchs that did not remain at the site (i.e. that were not recaptured), and of those that were recaptured, was their stopover duration influenced by either their size or their wing condition? We also looked for possible gender differences in stopovers (i.e. likelihood of stopover and/or duration of stopover as linked to gender of monarchs), that might explain the apparent male-biased sex ratio of the migratory cohort.

Methods

Study site

The data from this project come from a long-term study of monarch butterfly migration at Folly Beach, SC (32.6ºN, –79.9ºW), which is an approximately 10 km×1 km barrier island, oriented northeast—southwest, on the central South Carolina coast in Charleston County. Folly Beach is connected to the mainland (James Island) via the SC highway 171 causeway and is approximately 15 km from the city of Charleston. The vast majority of the island is under residential development with a small, localized business district near the island center. Further details of the study site, including habitat features, are given elsewhere (McCord & Davis, 2010).

Capturing monarchs

All monarchs were captured by the primary author (JWM), who lives on James Island and approximately 10 km from Folly Beach. Each year from August through December he captured (with a butterfly net) as many migrating monarchs as possible for the purposes of tagging them with uniquely numbered stickers from the MonarchWatch program (McCord & Davis, 2010). While there was no effort made to standardize the number of hours spent per day collecting (obtaining rates of capture per hour was not a goal of this project), JWM did spend more time collecting when monarchs were abundant at the site, which was typically from mid-October to mid-November (McCord & Davis, 2010). When a monarch was captured, JWM tagged it with a MonarchWatch sticker on the underside of the hindwing, recorded the gender, measured its forewing length and subjectively scored the condition of the wings on a scale of 1-5. In this system, 5 = excellent condition, no, or practically no, wear or damage, 4 = minimal damage/wear that presumably causes little immediate reduction in flying efficiency, 3 = moderate, damage significant enough to likely cause some reduction in flying efficiency, 2 = significant damage (often one wing-tip missing), causing labored flight, and 1 = major damage, flight extremely labored (usually with portion of both forewing tips missing and often with hindwing damage as well; Fig. 1). Importantly, when a previously-tagged monarch was spotted, JWM made every effort to capture it and note the tag number. For the purposes of the current paper, this allowed us to differentiate monarchs that were later recaptured at the site (following initial capture, i.e. 'stopover monarchs') from those that were never recaptured ('non-stopover monarchs'). All monarchs were released at the site of capture.

Data analysis

We initially used data from all captured monarchs to examine several possible factors that could influence whether or not the monarchs were later recaptured. We used logistic regression with the response variable being monarch later recaptured or not recaptured and with the year and gender as categorical predictors, along with wing length and wing condition being continuous covariates.

Figure 1. Scanned images of monarch butterflies representing all 5 categories of wing condition used in this project. See methods for description of criteria for assigning scores. Monarchs in category 5 had the freshest wings with no damage while those in category 1 had very worn wings with considerable damage.

Then, we compared the characteristics of monarchs (their size and condition) that were later recaptured to those that were not recaptured using general linear modeling, where wing length or condition (considered as a continuous variable) were response variables and recovery (yes or no) was a predictor, along with gender and year. Next, using the data from all monarchs that were recaptured we calculated the length of their stopover (in days) as the date of recapture minus the date of initial capture, plus 1 day (Davis & Garland, 2004). Because the actual dates of arrival to and departure from our site was not known for each monarch, these stopover 'length' values can be considered conservative estimates; actual stopover lengths are likely greater than what we calculated. To approximate a normal distribution these data were log-transformed. Then, log-transformed stopover length was the response variable in a general linear model that examined if year, gender, wing length or wing condition affected stopover lengths. All data were analyzed using Statistica 6.1 software (Statistica, 2003) and significance was accepted if $p<0.05$.

Results

From 1996 through to 2008, JWM captured and tagged 12,989 monarchs (Table 1). Of these, a total of 407 monarchs (3.1%) were later recaptured by him. The percentage of monarchs recaptured varied from year to year, with a low of 1.3% in 2000 to 5.6% in 2002. Moreover, results from the logistic regression analysis showed a significant effect of year on the likelihood of recapture (df=12, χ^2=55.2, $p<0.0001$). There was also a significant effect of gender in this analysis (df=1, χ^2=59.3, $p<0.0001$); the recapture rate for males (4.3%) was over twice that of females (1.8%), although the magnitude of this difference depended on the year (significant year x gender interaction effect; df=11, χ^2=20.8, p=0.036). Butterfly size (forewing length) was not significant (df=1, χ^2=0.8, p=0.348), however, wing condition was significant (df=1, χ^2=21.3, $p<0.0001$). The direction of the effect of wing condition on recapture rate can be seen in Table 2, where recapture rates of monarchs in all five wing condition categories are presented. The recapture rate was the highest (8.5%) for monarchs with the most worn and damaged wings (category 1), while the rate was the lowest (2.9%) for monarchs with the freshest wings with no damage (category 5).

In the direct comparison of wing lengths and condition of monarchs that were never recaptured to those that were recaptured, there was no significant difference in wing lengths ($F_{1,12729}$=0.05, p=0.823; Fig. 2A). While the gender and year parameters were not of particular interest in this test, there was an expected effect of gender ($F_{1,12729}$=160.63, $p<0.0001$; Fig. 2A), and a surprising effect of year ($F_{12,12729}$=15.33, $p<0.0001$) on wing lengths. The annual differences

Table 1. Summary of monarchs captured during all years, with proportions that were later recaptured (in the same season). The average length of stopover is shown for all years with standard deviations in parentheses.

Year	Total Captured	# Recaptured	% Recaptured	Stopover Length (d)
1996	961	36	3.7	4.8 (5.2)
1997	1,131	44	3.9	4.4 (3.1)
1998	285	8	2.8	7.3 (7.6)
1999	801	21	2.6	5.9 (7.0)
2000	758	10	1.3	5.1 (3.9)
2001	582	14	2.4	6.1 (6.7)
2002	1,809	102	5.6	3.3 (1.8)
2003	444	7	1.6	4.4 (4.4)
2004	395	19	4.8	6.8 (5.2)
2005	1,767	40	2.3	5.0 (3.0)
2006	1,542	29	1.9	5.0 (3.5)
2007	1,458	40	2.7	5.4 (5.2)
2008	1,056	37	3.5	6.2 (5.2)
Total	12,989	407	3.1	4.8 (4.3)

Table 2. Recapture rates of monarchs in all five wing condition categories assigned in this project. Score were such that a '5' represented wings that were fresh and undamaged and a '1' represented wings that were very worn and extremely damaged (see Fig. 1). Note that the total number of monarchs in this table (12,823) is lower than in Table 1 because 166 monarchs were not assigned a wing condition score.

Condition	# Captured	# Recaptured	% Recaptured
1	118	10	8.5
2	591	36	6.1
3	1,651	66	4.0
4	2,109	76	3.6
5	8,354	242	2.9

in wing lengths observed at this site will be examined in more detail in a subsequent manuscript. None of the two-way interaction effects were significant in the final model of wing length. Regarding the analysis of wing condition scores, we found that monarchs that were later recaptured had significantly lower condition scores (i.e. poorer condition) than those that were never recaptured ($F_{1,12780}$=5.65, p<0.0001; Fig. 2B), although the magnitude of this effect varied with gender (significant gender x capture interaction effect; $F_{1,12780}$=7.87, p=0.005). Again, other parameters in the model were significant, although not of primary importance for the current study; there was a main effect of gender ($F_{1,12780}$=25.09, p<0.0001) and year ($F_{12,12780}$=2.05, p=0.017) as well as significant gender x year ($F_{12,12780}$=3.67, p<0.0001) and year x capture ($F_{12,12780}$=2.58, p=0.002) interaction effects.

Finally, in the analyses of (log-transformed) stopover lengths (using all recaptured monarchs only), we found no significant effect of gender ($F_{1,380}$=1.23, p=0.267) on the number of days monarchs stayed at the site. However, there was an effect of year ($F_{12,380}$=2.70, p=0.0017). The annual variation in stopover lengths is readily seen in Table 1. The overall average length of stopover at this site was 4.8 days, but varied from 3.3 to 7.3 days. Importantly, there was a significant effect of wing size on stopover length ($F_{1,380}$=6.69, p=0.0100). Direct comparison of forewing length with (log) stopover length showed a weak negative relationship (r=-0.11, p=0.0206); smaller monarchs tended to have longer stopovers than larger ones. There was also a significant effect of wing condition on stopover length ($F_{1,380}$=16.66, p<0.0001), and this effect is evident in Figure 3, where average stopover lengths for each wing condition category are plotted. Monarchs with little or no wing damage tended to have shorter stopovers than those with moderate to high wing damage.

Discussion

One of the original goals of this study was to examine the characteristics of monarchs that stopover at this site in South Carolina and to determine if these individuals differ in any way from the general cohort that migrates through the site without stopping. In terms of wing size, stopover monarchs (those that were recaptured) did not differ from non-stopover monarchs; the initial decision to stopover or not is therefore not influenced by the size of the butterfly. However, of those that did stopover, smaller-winged individuals tended to remain longer at the site during stopovers, which is counter to the prior pattern where wing size did not influence recapture probability. The reason for this apparent discrepancy is not clear. It may be that size does not matter in terms of actual migratory flight behavior, but that for some reason, smaller individuals may require more time to forage and build their fat stores once on the ground. Regardless of the reason, if this phenomenon also occurs at other stopover sites along the entire migration pathway(s), one could expect the overall pace of migration to be somewhat slower for small monarchs than for large. This would be consistent with prior studies at other sites as well as our own, where large monarchs tend to predominate in the early phase of the migration period, with later monarchs tending to be small (Gibo & McCurdy, 1993; McCord & Davis, 2010).

Female monarchs appeared less likely to stopover at our site than did males (1.8% recapture rate for females vs. 4.3% for males). If this same pattern holds true for other locations in the migration pathway, it would suggest that females may differ from males in energetic requirements during migration (i.e. they need to stop less frequently than males). It is also not the case that females simply stay longer per given stopover bout (to compensate for fewer stopovers) since there was no gender difference in mean stopover lengths found here. This is consistent with data from another site in coastal Virginia (Davis & Garland, 2004). However, the original rationale for examining gender differences in stopover decisions was with respect to the disappearance of females from the migratory cohort (Davis & Rendon-Salinas, 2010). From the data gathered here, there is no evidence to support the idea that it is caused by females stopping more frequently or taking longer at stopovers than males. Prior analyses of data from this site also found no evidence for a gender bias in capturing monarchs; females were far fewer in roost collections as well as in those collected while nectaring (McCord & Davis, 2010). Thus there is apparently still no clear explanation for the decline of females among overwintering monarchs over the last three decades. It may be that the explanation does not lie anywhere in the migration itself, but before the migration even commences; future studies may need to examine the possibility that females are becoming less likely to enter the migratory cohort to begin with. This idea may be plausible given that work with other butterfly species indicates males have a higher tendency to enter diapause than females (Wiklund *et al.*, 1992, Soderlind & Nylin, 2011).

Results from all three sets of analyses in this study indicate that the condition of a monarch's wings greatly influences its migratory stopover decisions. At this stopover site, wing condition predicted the likelihood of recapture, butterflies that were later recaptured had poorer wing condition on average than those that were not recaptured (Fig. 2B), and wing condition affected the length of stopovers; the greater the damage, the longer the stopover (Fig. 3). These results are consistent with our expectations that individuals with damaged wings are at a disadvantage in terms of flight ability (which is known in other insects; Combes *et al.*, 2010; Dukas & Dukas, 2011), and that such may translate into reduced foraging ability during stopovers, thereby yielding the need to spend more time obtaining food and turning it into fat stores (Brower *et al.*, 2006). Alternatively, monarchs with damaged wings may require more fat reserves throughout the migration if they burn more energy flying than do undamaged individuals, and thus would need to devote a greater amount of time foraging at stopover sites to meet this need. This would also account for the greater likelihood of recapture (of monarchs with poor wing condition); this indicates that such individuals choose to stopover more frequently than those with no wing damage or wear.

If our results regarding wing condition can be generalized across most stopover locations throughout the migration flyways, they may have more far-reaching implications for the role of migration in "weeding-out" suboptimal individuals. If monarchs with damaged wings stop more frequently during the migration and for longer periods at all stopover locations, their overall migration pace would eventually become slowed. In fact many of these individuals may never reach the overwintering sites in central Mexico. Indeed, this may explain why in collections of monarchs at overwintering sites, the majority of monarchs appear to have relatively

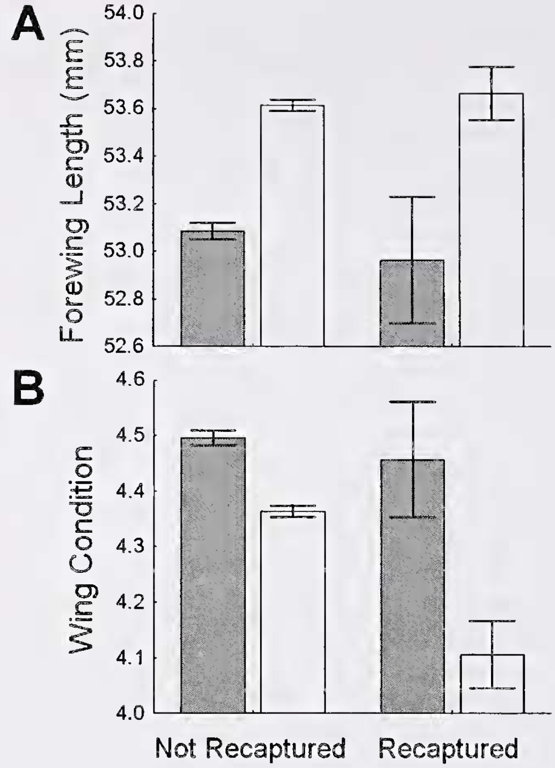

Figure 2. Average wing lengths (A) and wing condition scores (B) of monarchs that were never recaptured and that were later recaptured in the same season. Male (open columns) and female (grey columns) monarchs shown separately. Whiskers represent standard errors.

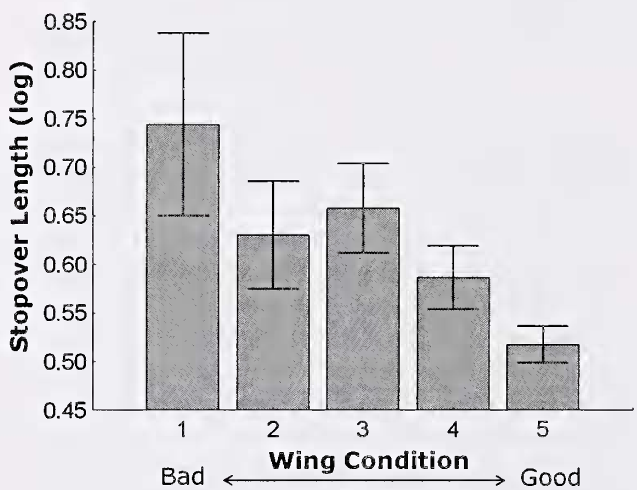

Figure 3. Average length of stopover (days, log-transformed) for monarchs assigned to each wing condition score in this project. Whiskers represent standard errors.

undamaged wings (A. K. Davis, unpubl. data).

There were certain aspects of stopover behavior at this site in South Carolina that are comparable to those found at a stopover site in coastal Virginia (Davis & Garland, 2004), despite there being only one year of data in that study (a later study at this site did not examine recaptures, Brindza *et al.*, 2008). First, the proportion of individuals that were later recaptured was nearly the same in both sites; out of 688 monarchs captured in one fall migration season at the Virginia site, 3.9% were recaptured, while at Folly Beach the overall rate was 3.1% across all years (although there was a degree of annual variation; Table 1). Second, the average length of stopover at Folly Beach was approximately 5 days. At the Virginia site it was approximately 3 days, using the same calculation for stopover length as the current study. These parameters (proportion recaptured and mean stopover length) should be easily obtained from other locations using similar methods, and in fact, we hope that future investigations of monarch stopover biology will strive to do this, especially in areas located in the central flyway which leads directly to the Mexican overwintering sites (Howard & Davis, 2009). This will allow for additional comparisons of stopover dynamics across a greater number of sites than is possible now. Moreover, this will also allow us to address more synthetic questions regarding monarch stopover, such as are monarchs more or less likely to stopover as the migration progresses southward, or are stopovers longer at locations near large water crossings?

Finally, we point out that this project serves as an excellent example of how monarch tagging can contribute to the scientific understanding of this species, as long as detailed records are kept and accurate data are recorded. Currently there are hundreds of individuals who tag many thousands of monarchs each year, but only for the purpose of having one of 'their' monarchs recovered in Mexico. As shown here, if records are kept on how many monarchs are recaptured at the site of tagging, these tagging activities would allow for a much greater breadth of questions to be addressed, and would broaden scientific understanding of the amazing migration of this species.

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